HILGARDIA

A JOURNAL OF AGRICULTURAL SCIENCE

PUBLISHED BY THE

CALIFORNIA AGRICULTURAL EXPERIMENT STATION

VOL. 1 NOVEMBER, 1925 No. 11

PHYSIOLOGICAL ASPECTS OF SOIL SOLUTION INVESTIGATIONS

BY

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INTRODUCTION

In investigations of the chemical system constituted by the soil and the plant, it is unavoidable, in the majority of cases, that the research should be directed into some specialized phase of soil chemistry, or of plant physiology. Little opportunity is afforded to make direct comparisons between soil conditions and the conditions of artificial cultures. For the past ten years, however, the California Experiment Station has conducted various soil and plant investigations which have made possible such comparisons. This has brought up for discussion numerous questions pertaining to the physiological aspects of soil solution investigations, and perhaps it is worth while to pause for a short time, in the course of detailed study of experiments, to take a general survey of several important physiological phases of the soil-plant system.

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* This discussion is based on papers submitted to the International Congress of Soil Science (Pédologie), Rome, May, 1924, and to the Western Society of Plant Nutrition, Stanford University, June, 1924, and Portland, June, 1925. It is intended simply as a critical statement of certain soil solution problems as they have presented themselves during investigations conducted in California; and its limitations preclude any but incidental references to the literature on the subject. In its preparation, discussions with my colleagues in California and with investigators in other institutions have been very helpful. Of especial value have been discussions of soil solution questions with Professor J. S. Burd and Mr. J. C. Martin, and of physiological problems with Professors C. B. Lipman, A. R. Davis and W. F. Gericke.

Physiological Relations of Soil Solution to Soil Organisms

Before proceeding with the main discussion, which concerns the higher plants, it seems indispensable to insert a brief statement regarding the physiological relations existing between the soil solution and the microörganisms of the soil. The statement that an essential condition of fertility in soils is the development of desirable microorganisms has been made countless times and in many forms. Yet this point may require new consideration in connection with current researches on the soil solution. The data obtained on water extracts of soils and the more striking and definite information made available by Burd and Martin[4] through their studies on soils with the use of a modified Parker displacement method, illustrate the fact that normally a soil solution is, in large measure, a biologically controlled system; that is to say, nearly all the anion (NO_3, SO_4, HCO_3) content of such a solution is of biological origin and equivalent quantities of cations must enter into solution along with the anions. If the hydrogen ion concentration remain unchanged, the principal cations involved would be K, Mg, and Ca. By thoroughly leaching a soil, its solution may be brought to a state of very low concentration and it appears that most of the essential ions cannot attain concentrations suitable for satisfactory plant growth in the absence of the biological formation of anions.

J. C. Martin and I have performed the following experiment which bears on this point. After leaching, different portions of a soil were placed in paraffined bottles with 5 parts of distilled water, and the suspensions were shaken several hours each day for nearly a year. In several of the bottles, the water was saturated with toluene. At the end of the period of contact, only a comparatively slight amount of material had entered into solution in the case of the toluene saturated water, while in the other bottles, where microbiological processes had proceeded actively, there had been a very striking increase in the concentration of the solution in contact with the soil. Recently, these biochemical relations have been made clearer by the the studies of Burd and his associates[1] on nitrification and denitrification in relation to the soil solutes. These same investigations also give evidence of the great importance of the biological formation of SO_4 anions in soils of the type studied. Apparently, we have every reason to reëmphasize the older teachings in terms of modern soil solution theories, and it may be suggested that from this point of view the study of the microörganisms themselves must find

its ultimate justification in establishing definite correlations between numbers or activities of the various types of organisms and the concentrations of the different ions of the soil solution. Likewise, it will be desirable to show that any control of the micro-population of the soil results in a corresponding control of the soil solution. It is evident that in connection with such researches, it will be of importance to conduct further investigations on the organic matter of the soil in its relation to the multiplication of different soil organisms and to the formation of nitrate, sulphate and bicarbonate anions.

Biological Action and Replaceable Bases

While the production of anions is accounted for primarily by the biological activities of microörganisms, the relative proportions of the different bases entering into solution to neutralize the acids formed are dependent to a very great extent, although not exclusively, upon the nature of those colloidal constituents of the soil involved in the replacement of bases. If these reactive compounds have had their calcium and magnesium too largely replaced by hydrogen, sodium, or trivalent bases, it cannot be expected that a satisfactory soil solution will be capable of formation, and of course, in the more extreme cases, some of the biological activities referred to above will themselves be inhibited. In the solution of the problem as a whole, it is evident that the study of biological activities and of the reactive silicates of the soil should go hand in hand. Both types of inquiry are essential in answering the basic question: Under what conditions can a soil produce an adequate soil solution? Fortunately, the development of the chemistry of replaceable bases has been very considerable and many soil problems have been clarified as a result of researches in this field. Much time also has been bestowed upon the investigation of various kinds of soil organisms, but no sufficiently comprehensive work has yet been reported dealing with these organisms and at the same time taking into account the effects of their activities on all the ions of the soil solution.

Nature of the Absorption of Essential Elements by Plants

Even in these brief preliminary statements, it has been found necessary to make two assumptions, first that plants absorb inorganic elements only from the soil solution, and, second, that the absorption is primarily concerned with ions. Probably these views are held by most plant investigators, though they have been questioned by some.

Whether these assumptions are correct or not, the investigation of the soil solution is necessary, but a serious complication would be introduced if it were shown that plants possess the power of making use of soil colloids directly. Fortunately, there seems to be no reason at present to believe that this particular complication must be met.

Several misapprehensions have arisen in some discussions of soil solution theories. Some writers have confused the soil extract with the soil solution, and deduced a concentration for the latter far lower than actually occurs in a fertile soil at optimum moisture content. Moreover, plants do not absorb the soil solution as a whole, but absorb the various essential elements from the soil solution. It is a very simple matter to show that plants can absorb ions and water differentially, so that it by no means follows that the total amount of water transpired necessarily limits the absorption of ions from dilute solutions. Perhaps it may be difficult to believe that a plant can obtain enough PO_4 from soil solutions which usually contain that particular ion in very low concentration, possibly only to the extent of one or two parts per million. However, solution culture experiments have demonstrated that a concentration of PO_4 of this order of magnitude may be adequate, provided that as fast as PO_4 is absorbed, more PO_4 is added to the solution, so that the concentration never falls below a critical level during those portions of the plant's growth cycle which require active absorption of phosphate.[16] In a good soil, this is exactly the condition which prevails. With regard to the absorption of iron, experience with solution cultures has demonstrated that colloidal iron compounds will not prevent chlorosis unless conditions permit of the actual solution of a small portion of the iron.

The ionic nature of absorption, of course, is not capable of direct and certain proof by any methods so far employed, especially because the whole question of the nature of ionization is being subjected to critical review on the part of the physical chemist. But, admitted this, it still appears that the most useful conception regards absorption by plants as being concerned with ions. The differential nature of absorption, the exchange of one ion for another in a solution during absorption, the dilute character of culture solutions, the affect of one element on the absorption of another and other considerations, seem to make it profitable to interpret results in terms of ions.[18] Certainly there is no advantage (other than convenience in preparation of solutions) in referring the composition of culture solutions to the salts which were originally employed, more or less arbitrarily. By calculating in terms of milliequivalents the composition of a culture

solution or the amounts of the elements absorbed therefrom, any possible inter-ionic relations will become apparent.

In pursuing this inquiry still further, it may be asked whether, in general, the concentration and composition of soil solutions from productive soils are of such a nature as to be adequate apart from the solid phase of the soil. The writer has had an opportunity to make just such comparisons by growing barley plants in artificial solutions side by side with plants grown in soils, the solutions of which were under investigation by Burd and Martin.[6] As a result of these comparisons, the question stated above can be answered in the affirmative. When a suitable amount of culture solution was used for each plant without change of solution after the earlier periods of growth, and when low concentrations of phosphate, maintained constant as far as possible, were employed, there was no difference of a really fundamental character between the artificial solutions and the soil solutions obtained by the displacement method. In both cases, the growth of the plants diminished the concentration of several of the principal ions while the concentration of HCO_3 was increased as the concentration of NO_3 decreased.

It is true, of course, that the technique of solution and sand cultures as ordinarily employed involves a somewhat different solution condition from that found in the soil, as will be pointed out later in connection with the concentration of PO_4 ions. Also, as a matter of convenience, it is frequently customary to change the culture solutions one or more times each week throughout the growth cycle of the plants. If they make good growth and if the volumes of solution are limited, it is probable that a very considerable reduction in concentration of various ions occurs during the intervals between changes of solution. This condition will be followed by a sudden change to a solution of the original concentration and the cycle will be repeated as often as the solutions are changed. In decided contrast to this condition is the one which appears to exist (at least as an average condition) in the soil solution of a cropped soil in which, notwithstanding many unpredictable fluctuations, the concentrations of several of the important ions decrease in a more or less gradual manner, and during the later stages of growth of barley and other plants, it may happen that for a considerable period of time, practically no nitrate remains in the soil solution.

Absorption at Different Growth Phases

These considerations suggest the importance of having suitable concentrations of essential ions available not merely at some time during the season, but at particular phases in the growth cycle of the plant. The work of Burd and Martin,[4] Stewart [28] and the writer,[14-17] seems to establish the fact that a very good barley crop can be obtained even when the soil solution has its concentration of NO_3 reduced to a negligible amount by the time of heading out of the plants, the fall in concentration of nitrate being accompanied by a less striking but significant fall in concentration of several other ions. As already stated, entirely analogous results have been obtained with artificial solution cultures.

It has even been suggested by Gericke,[10] on the basis of some interesting results obtained with solution cultures, that such a decrease in concentration of one or more essential elements is not only compatible with good growth, but is a necessary condition for optimum yield of crops. Although it is quite conceivable, especially in solution cultures, that an injuriously large absorption of one or more essential elements might occur or that the absorption might continue over too prolonged a period, it would be unsafe to advance at the present time too wide a generalization concerning these points, for one reason because the habits of growth of different types of plants, as well as climatic conditions, very greatly restrict the application of data obtained in any one particular experiment. One cannot disregard the question of a plant's ability to tiller or to branch in this connection. To give a specific illustration, the writer carried on an experiment with barley plants in which, because of the large volume of solution used for each plant, and the very frequent changes of solution, the concentrations of the various ions were maintained fairly constant throughout the growth cycle. The climatic conditions were very favorable, and the size of the plants grown in these solutions, in respect to total dry weight, number of tillers and amount of grain, was greater than that of plants produced during the same season by a fertile soil, even when the number of plants occupying each unit area of soil was much smaller than is customary in field practice. Likewise, the plants grown under the solution culture conditions just described were much larger than plants grown in those solutions which became reduced in concentration at the time of heading out. It is highly probable that different results might have been obtained with other types of plants possessing hereditary habits of growth which would have limited the amount of tillering or branching.

When an increased crop yield is obtained with plants like barley, by maintaining the original concentration of the culture solution throughout the season, the increase is largely dependent upon the production of successive cycles of growth, new tillers being formed over a considerable period of time and ripening being greatly delayed. (Each tiller might, of course, be regarded as a separate plant.) In general, such a situation would be entirely undesirable for plants grown under field conditions within a limited season. As a matter of fact, under a favorable climatic environment, it is very improbable that nitrate (and perhaps certain other ions) would ever be maintained in high concentration during the later stages of growth of a crop such as barley.* Burd and Martin[5] showed that even when a soil was liberally fertilized with nitrate, the concentration of this ion in the soil solution diminished during plant growth to practically as low a point as in a similar soil without treatment.

Assuming suitable moisture conditions, we may, therefore, regard it as a normal state for annual plants at least, that the concentration of the soil solution should decrease as growth proceeds, but it may be highly important, nevertheless, that appreciable, even though diminished concentrations of certain ions (for example, calcium), should be maintained in the later stages of growth, as has been shown by Gericke. It is increasingly evident that much of great value is yet to be learned about the effect of mineral elements at different stages of plant growth. The most clear-cut and convenient means of studying the question is by means of solution culture experiments. These are indeed indispensable, but the interpretation of the results of such experiments in terms of soil solution data and likewise the interpretation of data on the composition of the soil solution in terms of physiological response offer great difficulty, as I shall endeavor to point out.

Physiological Nature of the Soil Solution

Earlier in the discussion, an experiment was referred to in which excellent barley plants were grown in solutions containing very low concentrations of PO_4 ion. In almost every solution culture experiment heretofore reported, solutions have been employed with an initial concentration of PO_4 far higher, in some instances several hundred times higher, than the concentrations found in the soil solutions even of productive soils which have been investigated from this

* This statement may not hold for soils exceptionally high in easily decomposable organic matter.

point of view. Under solution culture conditions, because of this relatively high initial concentration, absorption of phosphate in the earlier stages of growth may be greater than under soil conditions and as a consequence the response to phosphate absorption in later stages of growth may be altered. At any rate, with regard to phosphate concentration, an important distinction exists between soil solutions and practically all artificial culture solutions so far described.

On the basis of experiments such as those mentioned earlier, I felt justified in making the previous statement that it is possible to obtain entirely satisfactory plant growth in certain artificial culture solutions differing from soil solutions in no fundamental way. This observation, however, does not imply that the presence of a solid phase is without effect on the absorption of mineral elements from a culture solution. We have compared the composition of plants grown in sand and in solution cultures, taking care to provide in both cases exactly the same volumes of solution for each plant. The plants grown in solution culture had higher percentages of nearly all the mineral elements present than the plants grown in sand cultures, although the latter developed the larger root systems. Obviously, the ease with which diffusion takes place in a solution culture had a marked influence on the absorption of the various ions. The retarding influence on diffusion must be manifested to an even greater extent in soil media than in sand culture media. The solution in contact with the solid medium acts toward the plant as would a more dilute solution in the absence of a solid. Probably, therefore, an inhibitory concentration would be lower in a solution culture than in a sand or soil culture.

We shall now continue, in a more detailed manner, the discussion of the physiological nature of soil solutions. It is first necessary to recall that Burd and Martin[6] have been able to obtain, from certain soils, solutions which give every indication of closely approximating the soil solution as it exists in these soils at optimum or lower moisture contents. The question which interests us in the present connection is the following: To what extent does the solution displaced from a mass of soil at a given moisture content represent the solution in actual contact with the absorbing membranes of the root system of the plant. In the first place, we must recognize the possibility that not all portions of a root system are equally active at any one time. There is formed, no doubt, as growth proceeds, a constantly advancing zone of actively absorbing root cells, the older portions of the root system becoming more or less inactive at least with some plants. Composite samples of soil representing various depths of a

cropped soil might, therefore, yield a composite soil solution derived from zones already more or less depleted by absorption, zones from which absorption was actively taking place and zones to which the roots had not yet penetrated. It is, perhaps, not entirely accurate to picture the soil solution of an entire mass of soil gradually becoming reduced in concentration. Possibly each absorbing root surface rapidly reduces the concentration of the soil solution immediately available, and this process continues as long as new root surfaces are formed and have access to fresh supplies of soil solution. Considering the plant as a whole, however, the supply of mineral elements would decrease as growth proceeds, if the mass of available soil were limited in amount, or if root growth ceased. In field practice, the extension of roots into deeper layers of soil and the character of the soil solution in these layers may sometimes have an important bearing on the absorption of mineral elements during the later stages of the growth cycle, as suggested by Crist and Weaver.[7]

It is difficult to say through how great distance ions can diffuse into the zone of the absorbing root membranes. In the main, the evidence indicates that it is the extension of the root system rather than the diffusion of ions to the roots which is of primary importance. Yet there must take place a considerable vertical movement of solutes along with capillary movement of water. Moreover, the application of water to the soil whether by means of rainfall or irrigation will, of course, have an important effect on the concentration of the soil solution in the various layers of the soil because of leaching processes.

While it is doubtful whether, by any method of dealing with masses of soil, it is possible to determine the exact composition of the solution in contact at any given moment with the active portions of the root system, still it can scarcely be questioned that soil solution studies are capable of demonstrating the general nature of the physiologically active solution and the tendency of plant growth to deplete such solutions. The practically complete removal of NO_3 from a limited mass of soil by barley and other crops proves that by one mechanism or another, the root system has a very efficient contact with the NO_3 ions of the entire soil solution. In this connection, it would be interesting to know how important is the differential diffusion of ions through the soil solution.

Additional emphasis should be given to the relation between the moisture content of a soil and the composition of its solution. The work so far carried out on certain California soils shows that there may exist at optimum and half optimum moisture an approximately inverse relation between moisture content and the concentration of

several important ions, but this inverse relation does not hold even approximately for all ions. Especially it does not apply to PO_4 ions, which may maintain nearly the same concentration at very different moisture contents. It follows, therefore, that every change in the moisture content of the soil brings about highly significant changes in the composition and concentration of the soil solution. It is, furthermore, obvious that under the soil conditions ordinarily obtaining during the growth of a crop in the field, the same moisture content of the soil is not maintained throughout. Moisture changes might, therefore, produce changes in the concentration of the soil solution with respect to certain ions, greater than those caused by the absorption of solutes by the plant. Even under the highly controlled conditions of tank experiments, it is scarcely possible to prevent fluctuations in moisture content, especially during periods of heavy transpiration.

These considerations introduce other matters of physiological import. It appears to be quite possible to determine how a soil solution is affected by changes in the moisture content of the soil, but this does not completely answer questions relating to the physiological response of the plant to such changes. At the lower moisture content, while concentrations of solutes would be increased, rates of diffusion might be decreased. Even leaving aside the influence of the solid phase, no simple relation can be established for the physiological effects of two solutions of different concentration. Absorption studies made on such solutions have indicated that over a given period the removal of ions from the more dilute solutions may be much greater than would be predicted on the basis of relative concentrations.

In the soil, the concentration and composition of the culture solution, the moisture, and the air supply, may all influence the development of the root system and therefore the total surface involved in the processes of absorption. This naturally alters the physiological relation of the plant to the soil solution, often perhaps in a highly significant manner.

Unfortunately, the problem, so far as the absorption of ions is concerned, is even more intricate, for the reason that the absorption of any given ion cannot be evaluated except in relation to the other ions present. Thus the rate of absorption of a cation may be influenced by the rate of absorption of the associated anion and conversely. Certain ions seem to be absorbed at a slower rate than others. Among the slowly absorbed ions are as a rule calcium, magnesium, and sulphate, but such general relations are likely to vary with different types of plants. It is possible that the nitrate ion has a special position, not

only because it is the source of nitrogen, but also because of its possible accelerating effects on the absorption of cations.

Clearly a knowledge of the composition of a soil solution or of an artificial culture solution does not, in itself, enable us to predict the rate at which each component ion will be absorbed or utilized by the plant.

The Supplying Power of the Soil

In any attempt to appraise the crop producing power of a soil on the basis of soil solution data, the dynamic nature of the soil and of the plant is, of course, a consideration of the utmost importance. It is essential to emphasize the supplying power of the soil, a concept which has been discussed recently by Livingston[21] in another connection The vital question is: Can the culture medium supply to the plant in each unit of time the required quota of every element needed at each particular phase of the growth cycle? According to the present view, many different soil solutions might fulfill this requirement, but obviously those of certain soils are deficient, in that the concentration of one or more essential ions falls so low that the amount absorbed in each unit of time becomes insufficient for the needs of the plant at some particular phase of growth. Theoretically, there are two general ways in which a soil might possess an adequate supplying power for essential elements: (*a*) A sufficient quantity of all the necessary elements for the total seasonal requirements of the plant might already be present in the soil solution of the total mass of soil at the beginning of the season. (*b*) The quantity of dissolved material present at any one time might be inadequate for these seasonal requirements, but additional amounts entering into solution might make up for any initial deficit. The first case can be illustrated by a sand culture in which the volume of solution and number of plants are so regulated that all elements (in suitable initial concentration) are added to the culture in the first instance in such amounts that the solution will maintain concentrations appropriate to each phase of growth. In a soil as it occurs in nature, the second method is necessarily involved, but to a degree varying for different elements. In the case of the phosphate ion, a plant presumably could obtain only a small part of its requirements for the whole growth cycle by the absorption of all the phosphate present at any given moment in the soil solution of the mass of accessible soil.

Several years ago, Burd[2] discussed this general question on the basis of data obtained on water extracts of a group of soils under intensive study. The conclusion was reached that there was always

present in water-soluble form in the whole mass of available soil, a sufficient total quantity of all the various essential elements for the requirements of a large crop at any period of growth. This was true even of a soil of relatively inferior crop-producing capacity. Of course, the total quantity of water soluble material present is not the only consideration since actively absorbing root surfaces are not at all times in actual contact with the entire internal surface of the soil, but furthermore, adequate supplying power evidently means the maintenance of certain minimum concentrations of each ion in the soil solution. Just what these minimum concentrations may be in any particular instance, we cannot say. Solution culture experiments show that often extremely low concentrations may suffice, if maintained in the solution for such periods as may be required by the plant. But the conditions for diffusion are so different in a soil that we are not justified in concluding that minimum concentrations in solution cultures and in soil solutions are necessarily the same. However, in this connection, results recently published by Burd and Martin[4] are of significance. The displaced solutions of a number of soils which had become depleted through continuous cropping were examined and compared with solutions of similar soils which had remained uncropped. Even at the beginning of the season the soil solutions of the cropped soils had very low concentrations of several ions (far lower than in the soil solution of the uncropped soils). It is not certain that these concentrations would be entirely adequate in a continuously renewed artificial culture solution, and certainly in the soil, it is not at all unreasonable to suppose that they might be too low to permit of the best growth of barley under a favorable climatic environment.

Briefly recapitulating, the supplying power of a soil interpreted as a physiological function, depends upon the following factors, among others: the concentration of ions in the soil solution at the time of initial contact with the absorbing roots, the suitability of the soil for root dispersion with the consequent increase in total absorbing surface, and the ability of the soil to maintain concentrations in the soil solution above critical minima for the different phases of growth, notwithstanding withdrawal by plants. We are not in a position at present to measure directly any one of these factors. Furthermore, we do not know to what extent surplus of an element stored in a plant during an early stage of growth can supply the requirements of the plant during later stages. Solution culture studies with barley have shown that a favorable medium during early stages of growth may cause abundant tillering. If then, the supply of certain elements is

exhausted too soon, none of these tillers can mature properly and the final growth is less satisfactory than if the supply of culture solution had been distributed over a longer period and growth confined to a few tillers.

The complexity of the situation might seem to render hopeless any attempt to interpret in terms of plant growth such data as can be obtained from soil solutions, yet encouraging correlations of this type have actually been obtained, even when the soil solution concentrations were computed very approximately from the results of analyses of one to five water extracts, particularly when comparisons of cropped and uncropped soils made at frequent intervals were used as a basis for estimating supplying power.

The fact of the matter is that plants possess in general a large measure of adaptability to their solution environment. It is perhaps impossible to learn the exact composition of the soil solution from which the actual absorption of ions takes place for reasons which have been set forth, but on the other hand *all the evidence at present available indicates that agricultural plants can make equally good growth in a very great variety of culture solutions.* Within wide limits at least, there is no evidence that plants thrive only in solutions with certain specific ratios existing between various elements. Davis[9] has reported definite experiments in support of this statement. While, therefore, it is true that every modification of the solution conditions is likely to induce a change in the composition of the crop, it does not follow that corresponding changes in the total crop yield will occur.

Nevertheless in cases which fall outside of this broad optimum range it is quite possible to obtain at least a general correlation between the composition and concentration of the soil solution and crop production, despite the inherent difficulties of determining the exact nature of the culture medium of a soil from a physiological point of view. It is at least reasonable to assume that considerable differences in crop production may be related to soil solution differences sufficiently striking to be made evident by the use of available methods of study, however imperfect these may be. It is only necessary that they should indicate when a decrease in supplying power for some element becomes a limiting factor, or when a toxic substance is present.

A complete discussion of the concept of the supplying power of a soil would include the oxygen and water supplying processes which are obviously of first importance and intimately bound up with the supplying power for ions. It would include also the influence of aerial conditions. No matter how self-evident, it is impossible to emphasize

too strongly or too often the fact that the adequacy of a soil solution is not an independent and fixed property of that solution, but is related to the other conditions affecting the growth of the plant and the rate of the absorption of ions, such as light, temperature and humidity. Recent researches warrant the statement that insufficient attention has been given to the light factor, especially as regards duration. The limitations of this paper, however, make it impossible to more than mention these phases of the discussion.

Specific Absorbing Powers of Different Types of Plants

One of the most interesting and important problems related to the physiological aspects of soil solution investigations concerns differences between various types of plants in regard to their ability to absorb mineral elements from the soil, sometimes referred to as the feeding powers of plants. Many hypotheses have been advanced to account for the recorded observations, but a critical review of the evidence now available convinces one that we are in possession of only a small portion of the data necessary to formulate any adequate theoretical basis for these phenomena. In any discussion of this kind, the first difficulty which presents itself is the precise meaning of the terms employed. Just what conception is conveyed by the expression absorbing or ''feeding'' power of a plant? It has been interpreted to mean various combinations of the following ideas:

(*a*) The difference in the percentage composition of different types of plants grown on the same soil.

(*b*) Differences in the rate of absorption of an element for each unit of surface of absorbing root membranes.

(*c*) Total quantities of an element removed from a unit area or volume of soil.

(*d*) Ability to bring into solution, by excretion of acid or disturbance of chemical equilibria, undissolved components of the soil.

(*e*) Ability to extend the root system into deeper layers of soil and thus draw on a larger total amount of soil solution.

These various interpretations may involve very different sets of processes and it will undoubtedly serve to clarify our view very much if we at least attempt to differentiate the phenomena involved.

When two types of plants are grown on the same soil, they are almost certain to have a different composition with reference to the elements obtained from the soil, but such facts do not enlighten us on the mechanism by which this difference came about. The roots

of the two plants might have been in contact with surfaces of different extent, or with different soil solutions, because of modifications produced in the solutions by the vital activities of the plants. The chance that the same amount of the same soil solution would be drawn on in each case is very remote. Moreover, the composition of the plant is, of course, related to the synthesis of carbohydrates in the aerial portions of the plant, the mineral elements being diluted, so to speak, to a different extent according to the kind of metabolism possessed by the particular plant, the stage of its growth, and the local variations of the environment. Where, therefore, the composition of two plants of different types grown on the same soil is found to be different, it is an interesting fact, but, one which so far has led to no important scientific conclusions. The accuracy of the facts themselves moreover is often open to question since the soil assumed to be uniform may, in fact, possess considerable variability as well as the individual plants.

If we grow plants in artificial culture solutions in such a way that we are assured that the roots of different types of plants are in contact with the same or nearly the same solution, we may observe in many cases that different types of absorption occur, but also that the composition of a plant of any given type can be changed to a striking degree by changing the composition of the culture solution. Consequently, when comparisons are made of plants grown in the same soil, not only do we not know the exact composition of their respective culture media, but we do not know to what extent the composition of the plant reflects a specific type of absorption, and to what extent it reflects merely the kind of soil solution which happened to be available under the particular conditions and which would vary from place to place and from time to time.

Differences in the rate of absorption of an ion for a unit area of absorbing surface, cannot be ascertained, in all probability, since there is no method by which the total extent of absorbing root area can be measured. It is a matter of common observation that some plants develop much more extensive root systems than others, but these comparisons have only a very limited value for the purposes now under consideration, since the general appearance and size of a root system is not necessarily an accurate index of the total active absorbing surface.

Comparisons of the total quantities of a slightly soluble element withdrawn by different crops from limited masses of the same soil may give some idea of the relative absorbing powers of the plants for the element in question, but the values will depend upon climatic conditions, and upon the adequacy of the supplying power of the soil

for other elements, and possibly upon the effects of the crops upon the development of microbiological activities.

One aspect of the absorbing power of plants which was earliest investigated had to do with the excretion of acids by plant roots. There is no doubt about the abundant excretion of carbon dioxide. The evidence of the excretion of other acids is in general negative, but this question is not yet settled. Great importance has usually been attached to the CO_2 excreted as a means of bringing into solution certain elements of the soil. Parker,[24] in a recent article, presents evidence which he believes tends to minimize the importance of CO_2 excretion. However, the experiments were conducted on one type of soil of a sandy character, and it is not certain that the use of a more highly colloidal soil would have given the same results. At any rate, it is very difficult at present not to regard the carbon dioxide excreted by plants or formed by microörganisms as of great significance, although the view of Parker may be correct that it is of less decisive influence on the comparative composition of different types of plants than has been supposed. Carbon dioxide excretion also may be concerned in another way in the absorption of ions. Nitrate ions, and possibly other anions under some circumstances, may be absorbed by many plants much more rapidly than the associated cations. The balance in the solution is maintained by the formation of HCO_3 ions. The metabolism involved in the production of carbon dioxide may, therefore, be of great consequence in this type of absorption.

The displacement of equilibria in the soil as a result of the absorption of ions by plants has been strongly emphasized in several of the best known theories regarding the relation of plants to the soil solution. It is scarcely a matter for argument that the plant does disturb the equilibria between soil mass and soil solution to a significant degree. For example, the removal of PO_4 ions by the growing plant displaces this particular equilibrium and causes more PO_4 to enter into solution. It has been suggested that the removal of calcium by a plant also plays a very significant role in the phosphate equilibrium. A certain support to this view is afforded by the experiments of Burd and Martin* in which they found that when hydrogen ion concentrations remained constant, the concentration of calcium in the soil solution had a marked influence on the phosphate concentration. As applied to the different abilities to remove phosphate from the soil, possessed by plants of different types, the critical data seem to be lacking. It should be shown, for example, that buckwheat, which is considered to have a special absorbing power for calcium, actually

* Burd, J. S., and Martin, J. C. Private communication.

lowers, or tends to lower, the concentration of calcium in the soil solution to a greater degree than barley or oats.* If this is found to be true where changes in hydrogen ion concentration do not intervene to overcome the effect, phosphate concentrations should increase and the plant having the greater ability to lower the concentration of calcium should have an opportunity to absorb phosphate from a solution with a higher concentration of this ion, or at least a larger quantity should enter into solution and be absorbed by the plant in each unit of time. In this sense and probably only in this sense, the plant would be utilizing the undissolved phosphate of the soil.

The whole problem would be simplified if we could explain all of the relations of the plant to the soil on the basis of chemical equilibria and mass action effects. Unfortunately, biological systems do not fit completely into such a scheme. It does not seem possible to escape the conclusion that a plant cell may effect the movement of ions against a concentration gradient, involving the expenditure of energy by some mechanism as yet unexplained. Experiments on the aquatic plants Nitella and Valonia, have offered a clear picture of the general situation.

In studying the absorption of ions, it is important to recognize that a plant holds a large percentage of its inorganic elements in soluble form. Certain elements may be accumulated in a plant in large amounts without any evidence that an organic combination or a precipitation has been effected, except as regards a very small proportion of the total quantity present. On the other hand, much has been written concerning the accumulation of calcium in plant tissue in insoluble form. A striking instance of this insolubility, observed in our own investigations, is shown by the buckwheat plant, in which nearly all of the calcium may be insoluble in water. This fact, in itself, does not justify us in assuming that the insoluble calcium is necessarily in the form of calcium oxalate or similar compounds. It still remains to be determined to what extent poisonous organic acids requiring precipitation with calcium, are developed in agricultural plants. While buckwheat apparently contains nearly all of the calcium in water-insoluble form, Reed and Haas[27] have found as high as 60 per cent of soluble calcium in the leaves of citrus plants, which also are considered to have a marked power of absorbing calcium and which show great injury when the supply of calcium is too low. It has been suggested that the relatively high hydrogen ion concentration reported for the sap obtained from buckwheat plants may have an important bearing on their calcium absorbing power, but the hydro-

* Experiments of this type are now being carried out in this laboratory.

gen ion concentrations reported by Reed and Haas for citrus leaves show an intensity of acidity very similar to that of barley. These are only a few instances of the contradictions which are met with in attempting to offer any general explanation of the absorbing power of plants for ions on a basis of simple chemical equilibria.

It will be well at this point to comment on the hydrogen ion concentration of expressed plant saps. It is evident that the interpretation of such data is subject to very definite limitations, because an expressed sap is a mixture derived from many types of cells, both living and dead. Changes in reaction brought about under changes in environmental conditions might result from alteration in the relative proportions of cells of different reactions rather than from changes in the reactions of cells of any given type. The surprising thing is, not that sight fluctuations of hydrogen ion concentration have been noted when plants have been grown under diverse influences, but rather that the reactions tend toward such constant values, as a general rule. A striking illustration of this is afforded by the experiments of Reed and Haas, in which citrus trees were grown in solutions of extreme types without any significant modifications of the reaction (H-ion concentration) of the sap expressed from the leaves, although the chemical composition of the tissues was influenced in a very marked way by some of the culture solutions employed.

Minimum Requirements of Plants

Another phase of the specific adaptations of different types of plants to the same soil solution, already mentioned incidentally, may well merit more attention. It seems to be quite true that many types of plants may grow at an optimum rate in the same kind of solution, when the composition of the solution and the rates of renewal are such that no deficiency in the supply of any element can occur. Undoubtedly, under these circumstances, some elements will be absorbed in amounts greater than necessary for growth. It is, of course, by no means true that plants absorb only what they need.

The minimum percentage of any inorganic element which can occur in a normal plant tissue will differ with different types of plants, as has been suggested, for example, by the recent work of Jones and Pember,[19] and Pember and McLean.[25] This fact might seem to afford a basis for the determination of deficiencies in culture media by the chemical analysis of plants. After accumulating a sufficient amount of data on plants grown under controlled conditions, it is reasonable perhaps to assume that some hope exists for certain

correlations of this kind, yet here again we have to deal with a maze of interreacting systems. It is only necessary to mention such difficulties of interpretation as those involved in the effects of one ion on the absorption of another, the possible limited replacement of one element by another in physiological processes, and the probable effect of climatic conditions on the minimum percentages of an inorganic element capable of existing in plant tissues. Yet we have reason to believe that some plants grow better than others on a poor soil, because they can produce a greater dry weight for a given quantity of some element which exists in the soil moisture, or is renewed therein in low concentration.

Sometimes perhaps the adaptation of a plant to a poor soil is concerned with the length of the growth cycle in relation to the ability of the soil to supply essential elements to the soil moisture, and therefore to the plant. A plant with a short period of growth might be adapted to a limited supply or very early exhaustion of some essential element in the soil. On the other hand, a plant with a rapid rate of growth and a comparatively extended growth cycle might require soil in which a high rate of supply could be maintained over a longer period. Here, as in every phase of soil solution investigations, physiological problems demand study.

Probably nearly every one would agree now to the statement that a "best" solution does not exist for any plant in the sense in which this term is ordinarily used. In another sense a "best" solution or limited number of "best" solutions might be conceived. If each essential element could be assigned some definite value on a unit basis, somewhat after the manner of evaluating fertilizers, then the best solutions would be those producing the largest dry weights of crop for the smallest total values, corresponding to the essential elements absorbed. Practically a determination of this sort might not be feasible because of climatic and other complications referred to above. The point it is desired to emphasize is that many culture solutions of very different composition may all be equally favorable to plant growth, but some solutions may be more economical than others. If there is to be a search for best solutions, it would seem that it must be based on this idea of economy. Incidentally, it may be remarked that even if a best or most economical solution could be worked out for each phase of growth of a certain crop, it is not apparent how such a condition could be established practically in soil solutions.

The recognition of the effect of one ion on another in absorption processes does not in any way support an assumption that an element can be absorbed or utilized only in some particular ratio to another

element absorbed at the same time. Nitrate, for example, may be absorbed readily from solutions of any non-toxic nitrate. It is, of course, obvious that the utilization of nitrate for growth will depend upon the adequacy of the supply of all essential elements. Thus, relatively large amounts of both potassium and nitrate may be required at certain stages of growth of cereal plants, but this is not evidence that these ions necessarily must be absorbed or utilized in chemically equivalent quantities. During plant growth, an extraordinarily complex series of chemical reactions may involve the various essential elements and we are totally unable to say at the present time how directly or how indirectly any two elements may function together in the metabolism of the plant. We can say only that lack of a sufficient quantity of some essential element may disturb the whole chain of processes or alter the internal solution environment by which metabolic reactions are influenced.

These points are discussed now, for the reason that they focus attention on the deficiency of our knowledge with reference to one indispensable phase of the study of soil and plant relations, namely, the functions of the essential elements in the synthesis of organic compounds by the plant, and the possible differences which may exist between different types of plants in this regard, either in kind or degree. Not only quantity but also quality must be considered. In general, one cannot say to what extent or why alterations in the composition of the soil solution modify the desirable qualities of the commercially important portion of a crop. The most denite information available concerns the possibility of changing the protein content of wheat by supplying nitrate at appropriate growth phases, as evidenced by the investigations of Gericke,[11] Davidson and Le Clerc,[8] and of others.

If the analysis of the problem of absorbing powers of different plants as given above is correct then we are justified in suggesting that while certain well-defined avenues of approach toward a solution are indicated, the need of the present is for data obtained under the most careful conditions of control practicable. The advancing of additional general theories may well await the results of the necessary experimentation.

Soil Acidity and Plant Growth

There is probably no phase of soil and plant relations which has received more attention than the influence of soil acidity on plant growth. Since the introduction of the hydrogen electrode into agricultural chemical laboratories, the investigation of hydrogen ion con-

centrations of soils has become exceedingly popular. It cannot be denied that the hydrogen ion concentration of soil solutions is an extremely important variable, one that must always be taken into account, but it should never be forgotten that many other factors may vary concurrently with variations in the hydrogen ion concentrations. If we determine this value alone, it may be a very hazardous assumption that the observed plant growth or distribution of species is correlated directly and exclusively with hydrogen ion concentration.

After all, how often do we really determine the physiologically effective pH of a soil solution? Nearly all pH values reported so far have been determined on soil suspensions. In some investigations, it has been found that within wide limits, the proportion of water to soil had but little influence on the reaction of acid soils. As the investigations are extended to include an increasing number of soils, instances are being reported in which changing the proportion of water does make an appreciable difference in the reaction of the suspension. Probably this should be expected in view of our present knowledge of soil solutions and soil extracts. The solid phase would be in equilibrium with a different solution for each proportion of water, which might result in an alteration in the amount of acid substances dissolved or in the extent of their hydrolysis. But suppose, instead of using a soil suspension, that we determine the pH of a solution displaced from a soil at a desired moisture content, are we then in a position to state that the reaction as determined is of exact physiological significance? Clearly, we are faced with the same difficulties of interpretation that have already been described with reference to the general composition of the soil solution.

The soil solution displaced from a mass of soil may have a certain definite intensity of acidity, but the question arises, are all of the absorbing root cells actually in contact with a solution of the same acidity as that possessed by the displaced solution? If the soil solution of an acid soil contains nitrate, then as plant growth proceeds, the tendency, according to solution and soil culture data, now available, would be for the solution to change its reaction in the direction of a decrease in the intensity of acidity. Therefore, if the soil solution is to exert its characteristic hydrogen ion concentration, the processes of diffusion and of solution would have to keep pace with the tendency of the plant to change the reaction of the solution. It is by no means certain that this would be the case, since a rapidly growing plant has a very marked ability to bring about changes of reaction, according to the data reported by Theron[29] and by others.

If a soil suspension shows an alkaline reaction, as determined by the usual methods, it is still more open to question whether the reaction of the soil solution immediately affecting the plant roots has the same alkaline reaction as that of the suspension, or even that of the displaced solution. In this system, the influence of the carbon dioxide given off by the plant roots, as well as that developed by the activities of microörganisms is of importance. The reaction in such systems is determined to a large degree by the equilibrium existing between CO_3-, HCO_3-, and CO_2. The percentage of CO_2 in the soil atmosphere is generally much higher than in the outside atmosphere and this higher concentration tends to reduce the alkalinity of the soil solution. In certain experiments I have found that the displaced solution of an approximately neutral soil (under crop) which had received a heavy application of calcium carbonate was slightly acid, and that the reaction became strongly alkaline after boiling the solution. The reaction of the films of solution in immediate contact with root surfaces actively producing CO_2 might have possessed a still different reaction. The fact that plants grow well in soils showing, under certain experimental conditions, a distinctly alkaline reaction in their suspensions, does not, in itself, prove that the plants make their best growth in alkaline solutions.*

If we leave aside the complications of the soil and turn to the results of solution culture experiments, we find that the preponderance of evidence does not indicate that acidity of the order of pH 5 to 6 is inimical to the growth of common agricultural crops. It is certainly true that many soils of a similar intensity of acidity are improved by liming, but various other changes occur when lime is added, besides the lowering of hydrogen ion concentration.

In the first place, the acid reaction may be indicative of an absence of calcium in the solid phase of the soil in replaceable form by which the soil solution could be replenished. Therefore, a plant might be unable to obtain from such a solution the required amount of this element. It is easy to understand that an acid soil might be unfavorable to plant growth simply on account of lack of calcium, while a culture solution of similar intensity of acidity containing an adequate concentration of calcium might present an entirely favorable medium. The importance of calcium supply in connection with acid soil solutions has been emphasized by Truog[30] and others.

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* Compare disccussion by W. H. Pierre (Soil Science, 1925, xx, 285–305), published since this article was written. The data presented by Pierre emphasize a somewhat different point of view, but are not necessarily inconsistent with the opinions advanced above.

In relation to the calcium factor in acid soils, it is especially useful to interpret conditions in terms of the theory of replaceable bases, as has been done by various European investigators and by Kelley and others in America. An acid soil, during the process of its formation, may have had much of its replaceable calcium substituted by hydrogen, and thus a soil solution in equilibrium with such a system might have too low a calcium concentration from a physiological point of view. This conception emphasizes the inability of such a soil to maintain suitable concentrations of calcium in the soil solution. Of course, the nature of the plant cannot be disregarded. Some plants may grow well even in a solution markedly deficient in calcium for most agricultural plants. This adaptation may be related to some special ability for absorbing an adequate supply of calcium from a solution of exceptionally low concentration with respect to that element, or perhaps to a lower requirement for calcium on the part of the plant.

The importance of supplying the plant with an adequate concentration of calcium does not necessarily imply that the calcium must exist originally in the solution as calcium carbonate or bicarbonate for the purpose of neutralizing acids developed by the plant. Unquestionably the plant has a marked ability to develop bicarbonates from solutions containing nitrate. Since the nitrate ion may undergo complete transformation in the plant, residues of basic properties would be provided through biological processes even though the culture solution contained no carbonates or bicarbonates originally. Furthermore, in the buffer system of the plant, other cations than calcium may play an essential role. When nitrogen is supplied only in the form of ammonium salts, it may become necessary to add bicarbonate to the culture medium since the rapid absorption of ammonium tends to bring about too great a concentration of hydrogen ions.

The effect of hydrogen ion concentration on the absorption of other ions merits further investigation. Certain experiments have indicated that in complete culture solutions of an acid reaction, the total equivalents of anions (including NO_3) absorbed may exceed those of cations, the intensity of acidity in the solution being decreased usually to a point close to neutrality. With alkaline solutions, the reverse process may occur. (The excretion of CO_2 by roots, as well as the differential absorption is, of course, of primary importance in both processes.) As Reed and Haas point out, these findings may not apply to all plants nor to every ion. The investigators referred to did not find, for example, that Cl was absorbed by citrus trees more rapidly from an acid solution than from an alkaline one. It is probable that the effect of reaction on absorption is especially important in connection

with absorption of nitrate ions and the carbonate-bicarbonate equilibrium. In any case, it is certainly true that no simple application of an isoelectric point theory can be made, so far as ion absorption is concerned.

Much evidence has been advanced tending to show that in addition to the effect of reaction on normal metabolism, some acid soils are inhibitive of plant growth because of toxic concentrations of aluminum or iron. Additional factors, such as the influence of reaction on micro-organisms, presence of toxic organic compounds, etc., have also received attention. While attempts have been made from time to time to emphasize the complex nature of the physiological phenomena involved in the study of acid soils, universal recognition has not yet been accorded the importance of differentiating clearly between the various factors.

Alkaline Solutions and Plant Growth

Under solution culture conditions, it has very frequently been observed that solutions of an alkaline reaction are less favorable to the growth of annual plants than slightly acid solutions. At alkalinities represented by pH 9 or above, distinct injury may occur. It is now necessary to inquire whether the unfavorable nature of an alkaline solution is solely attributable to the increased concentration of OH ions.

This is not an easy question to answer since it is difficult or impossible to maintain in alkaline solutions the desired concentration of calcium, magnesium, phosphate and iron. The fact that numerous plants make excellent growth without the slightest evidence of injury in certain acid solutions proves definitely that such concentrations of H ion are not unfavorable *per se*, but the inhibited growth in an alkaline solution does not, of necessity, prove that the hydroxyl ions are toxic. Undoubtedly the limitation of the concentrations of calcium and iron in complete culture solutions of alkaline reaction may be influential in restricting or preventing plant development. Theron,[29] however, working with a culture solution of such a composition that the reaction could be varied over a wide range, still found an alkaline reaction to be less favorable than a slightly acid reaction. Reed and Haas,[26] on the other hand, found that walnut seedlings were extraordinarily sensitive to an absence of calcium in the culture solution, and that solutions of pH 8 to 9 were not especially harmful provided calcium were present as, for example, in solutions of calcium hydrate. (However, solutions with pH values much above 9 were stated to be toxic.)

It is undoubtedly true that different species of plants have markedly different degrees of tolerance to alkaline solutions, including both the high OH ion concentration and the deficient concentrations of certain of the essential ions. In soils, a very high pH value is almost certain evidence that the soil solution has a deficiency of supplying power for one or more ions. While, therefore, much more study of the mechanism of injury is required, the emphasis on the generally unfavorable nature of highly alkaline solutions is justified.

A brief comment should be made concerning the difficulty of maintaining desired pH values in alkaline culture solutions. Once started, the plant has a striking tendency to reduce the original alkalinity, and there may be, also, an appreciable difference of reaction between the body of the solution and the solution in immediate contact with the root system. It is especially difficult to draw conclusions when sand cultures are used. In such experiments, the total volume of solution applied to the sand may be limited in amount and it is quite probable that the alkaline reaction may be reduced in intensity with extreme rapidity, especially in the films of solution surrounding the roots. It will also be found that the sand itself, however purified, tends to reduce the alkalinity of the culture solution.

Methods of Investigating the Physiological Effects of Soil Reaction

Notwithstanding the enormous volume of literature pertaining to soil acidity, experiments of the most decisive type are still lacking. Such experiments would include a very extensive series of observations on the displaced solutions or water extracts of many different soils of acid reaction. The soil solution data should be obtained, not merely for one sampling, but at intervals throughout the period of growth of several typical crops. The concentrations of the principal essential elements and of hydrogen ions should be determined and also the concentrations of aluminum, iron and manganese, as well as the oxygen supplying power (Hutchins and Livingstone)[18] of the soil, or its reduction potential as suggested by Gillespie.[12] Further application should be made of present knowledge regarding the exchange of bases. It would not be sufficient to confine the experiment to field studies, but large quantities of soil should be made homogeneous and pot or tank experiments should be arranged so as to permit of strict control of moisture conditions, aeration, etc. A properly conducted investigation, it will readily be granted, would tax the resources of an experiment station, yet the expenditure required would be but a small frac-

tion of the sums which have been spent in the past on various field tests on acid soils. Furthermore, it is essential to have much more definite evidence than we now possess concerning the nature of the soil solutions of various acid soils which have been observed to respond in different ways to lime applications.

The numerous lime requirement methods, even though useful as empirical guides for lime application when correlated with field tests, certainly do not clarify very materially the physiological problems involved. It is no longer held that lime must always be used to the point of neutrality. Occasionally reports have been made of unfavorable effects produced by adding large quantities of lime to acid soils, and certain acid soils apparently do not require lime even for the growth of leguminous crops. Evidently a lime requirement method is of very slight assistance in analyzing the physiological condition of an acid soil solution before and after liming. What we really need to know is the quantity of lime required to bring the soil solution to a physiologically suitable composition for a given crop, not merely with regard to hydrogen ion concentration, but also with reference to the concentration of calcium, magnesium, phosphate, nitrate, or of other essential ions, also of toxic substances. All of these studies would be intimately bound up with a consideration of the effect of liming on biological activities, because of the relation of the latter to the soil solution.

Alkali Soil Conditions

The soil conditions commonly referred to under the general term of "alkàli" present, in many parts of the world, an exceedingly important special field of investigation, yet it is well to emphasize the view that the study of alkali soils is not set apart from the study of soils in general. In large measure, the general methods of attack and the basic phenomena are the same throughout. In alkali soils, as well as in other soils, we must determine the reaction, concentration, and composition of the soil solution in order to arrive at an understanding of the physiology of inhibited growth. It is true that frequently, in such soils, the physical state of the soil may be the primary limiting factor, but this condition also is to an appreciable extent determined by, or at least reflects, the character of the soil solution. In alkali soil solutions, we must sometimes take into account excessive concentrations of certain ions or undissociated salts, but it is equally important to ascertain whether any of the essential ions may not be present in too low concentration (for example, Ca or Fe), as a result perhaps of high alkalinity or of the character of the bases combined in the

silicate colloids. This general question has been too fully developed in recent papers to require further discussion here. The few remarks which have just been made are intended to suggest that physiological studies of alkali soils must follow the course required of all investigations of soil and plant interrelations, including experiments with artificial culture solutions interpreted with reference to data on soil solutions.

The Number of Elements Essential for Plant Growth

In the vast majority of soil and plant investigations, no attention has been given to chemical elements outside the list of those commonly thought to comprise the essential elements for plant growth. We may now regard this list as definitely proved to be incomplete. The work of Mazé,[22] the Rothamsted Experimental Station,[31] McHargue,[23] and Lipman and Sommers,* makes it necessary to include additional elements, such as manganese, boron, silicon, and perhaps numerous others, at least for the experimental conditions used by these investigators. The investigations in this field will require much extension, but the point may now be raised whether all naturally occuring soil solutions necessarily contain adequate concentrations of all of these rarer or less recognized elements, or if so, what influence on plant growth or efficiency of utilization of other elements would be produced by increasing the minute concentrations already present? It is apparent that the almost overwhelming complexities of the study of plant growth will be increased by the necessity of explaining the function of various chemical elements overlooked in the earlier history of plant investigations.

The statement may be ventured that no completely satisfactory solution of the problem of the function of any of the essential elements can be realized until the present or future discoveries of the physicist and chemist concerning the structure of the different chemical atoms are capable of being utilized by the biochemist.

Possible Extensions of Soil Solution Investigations

The discussion thus far has been an attempt to present some phases of the physiological relations of plants and soils from the point of view of scientific research. Before closing, I desire to add several comments on the possibility of making practical application of researches of this type. In the first place, it will readily be admitted that there is not

* Lipman, C. B., and Sommer, A. L. 1924. Private communication.

available at the present time any scientific method by which it can be predicted under field conditions whether or not a given soil can develop an adequate soil solution, or whether a certain system of management or fertilization will correct deficiencies. This statement, of course, does not deny the practical value of local empirical tests, especially when guided by scientific findings. Such tests are generally the best means for arriving at a decision concerning an immediate program of local soil improvement. Under the most favorable circumstances, therefore, they may be of great practical use, notwithstanding the fact that scientific reasons for observed effects may remain entirely undisclosed. The danger which inheres in field tests is that attempts may be made to generalize from them too widely. It appears that sufficient emphasis has not always been placed on the limited and local character of a majority of these tests.

To what extent may it become possible to apply in the field the results and methods of intensive investigations of soils and plants, such as have been discussed in this article? Obviously, it would be useless to obtain haphazard samples of soil from the field for the purpose of studying the soil solution, because of the variability of soils and especially because of rapid seasonal changes in the soil solutions. However, it does not necessarily follow that field investigations are beyond the range of possibilities. On the contrary, it may become desirable, sooner or later, to attempt studies of soil solutions under field conditions, in selected areas in which general observation suggests that some particularly favorable or unfavorable relation exists between crop and soil solution. In each investigation of this type, it would have to be determined how samples should be taken so as to avoid any objections based on soil variability or seasonal fluctuations. These factors can never be left out of consideration, yet by the use of statistical methods and with sufficient data, it is reasonable to suppose that important correlations may be discovered. The time factor would require very careful consideration. It must be realized that a plant is not in contact with a soil solution for an hour or day only, but over the whole season and that a soil solution at one time may be completely different from the solution of the same soil at another time.

Unfortunately, the problem is made especially difficult because the character of the soil and therefore of the soil solution is not ordinarily homogeneous in different layers. In the case of certain crops, it may be very difficult to determine the exact location of the actively absorbing root system. Then, too, physical conditions in the soil may interfere with root dispersion and the limitation of growth may

be chiefly a question of total available internal surface rather than of the character of the soil solution present in any given mass of soil. Certainly, it is not probable that any soil solution studies at present feasible are sufficient to explain fully the observed growth of plants on different types of soil. These remarks are particularly cogent when applied to agriculture under arid conditions where moisture relations as such are often of such critical importance.

It is not to be supposed, therefore, that intensive investigations of soils will ever entirely replace empirical tests for local guidance in soil treatment, or for the determination of the crops adapted to a given soil type. Rather, it must be the function of the controlled experiments to seek to explain the main features of crop response, to determine the cause of malnutrition, to suggest possibly new kinds of local tests and especially to establish principles which shall indicate some of the ultimate effects of the various types of soil treatment. Finally there always remains the possibility that a thorough scientific knowledge of soil and plant relations may make possible some striking practical applications at present unforeseen.

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